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Temporal and depth-associated changes in the structure, morphometry and production of near-pristine *Zostera marina* meadows in western Ireland

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ABSTRACT

The eelgrass *Zostera marina* is a dominant, subtidal meadow-forming seagrass in temperate regions in the northern hemisphere. Due to the numerous ecological services they provide, seagrass systems rank amongst the most valuable ecosystems worldwide but there is a lack of data regarding the structure and productivity of Irish seagrass populations. To address this gap, this investigation assessed temporal changes and depth acclimations of vegetative parameters, such as, shoot length and weight, shoot density, seagrass cover and below- and above-ground biomass, in three near-pristine subtidal *Z. marina* meadows in western Ireland. Most parameters revealed a marked temporal pattern, displaying clear unimodal responses, with peaks attained in July, intermediate values in April and November, and lowest values observed in January. Moreover, eelgrass cover and density decreased from 76.1 ± 6.5% in shallow meadows to 34 ± 4.5% at greater depths; inversely, other parameters such as shoot biomass or shoot length increased 2–3-fold with depth. Furthermore, annual leaf formation rates and above-ground biomass were estimated and compared to those of eelgrass populations from different latitudes (28°–66°) reported in the literature. Results suggest that the vegetative development of Irish populations corresponds to global data reported at different local and global scales of *Z. marina* populations inhabiting stable environments; our data serve as a first baseline for the assessment of potential future environmental impacts, including climate change and eutrophication.

1. Introduction

The study of keystone species is vital for biological management and conservation, in particular in view of currently observed impacts of global change, including anthropogenic disturbances and climatic environmental shifts (Thomas et al., 2004). Significant impacts at community and ecosystem level have been documented over the last few decades, so that there is a critical requirement for species monitoring and the preservation of key environmental indicators (Hoegh-Guldberg and Bruno, 2010). Non-polluted and undisturbed areas have been widely used as a baseline to monitor habitat disturbances and degradation; however, nowadays there is a lack of pristine environments, particularly in marine coastal ecosystems due to exposure to direct and indirect human pressures (Jackson et al., 2001; Knowlton and Jackson, 2008).

Seagrasses are angiosperms that complete their life cycle within marine environments and that are typically associated with sheltered and shallow habitats (Hemminga and Duarte, 2000). These macrophyte communities rank among the ecologically most valuable ecosystems worldwide due to the numerous services they provide, such as shoreline protection, habitat and nursery grounds, high oxygen and biomass productivity and carbon sequestration (e.g., Costanza et al., 1997; Fourqurean et al., 2012). However, they do not enjoy the international and social recognition as other charismatic ecosystems such as coral reefs or tropical forests (e.g. Nordlund et al., 2018). In temperate regions of the northern hemisphere, one of the main meadow-forming seagrasses is the eelgrass, *Zostera marina* Linnaeus. Displaying a broad distribution from subtropical regions to the Arctic Circle, between 27° and 70 °N, the species is adapted to a wide range of temperature regimes, from -1 °C in Arctic regions, to 30 °C in subtropical areas (Ibarra-

Abbreviations: LM, Lettermore; TI, Tír an Fhia; FV, Finavarra; T1, transect 1; T2, transect 2; SST, sea surface temperature; BG, below-ground; AB, above-ground; CV, coefficient of variation

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Obando et al., 1997; Olesen et al., 2015; Ruiz et al., 2015). This adaptability renders *Z. marina* an exceptionally plastic character with regard to vegetative growth, life cycle and reproductive effort (i.e., Keddy, 1987; Meling-lópez and Ibarra-Obando, 1999).

Temperature and irradiance have been identified as the most relevant factors driving temporal variations of temperate seagrasses; they control metabolic processes such as photosynthesis and respiration (e.g., Zimmerman et al., 1995; Marsh et al., 1986; Sang and Park, 2005), but also affect the population structure, *flowering and seed germination* (i.e., Durako and Moffler, 1987; Diaz-Almela and Marbà, 2007; Moore et al., 1993; Stubler et al., 2017). Temperate eelgrasses typically exhibit marked seasonal growth, with optimal productivity rates observed during warmer periods with higher daylight hours during which leaf structures increase in biomass and size, allowing enhanced photosynthetic performance and subsequent storage of energy-rich compounds such as carbohydrates, mainly below-ground (Alcoverro et al., 2001). On the contrary, in colder and darker periods, seagrass shoot size decreases, thus reducing photosynthetic tissues, resulting in low metabolic rates and the utilisation of existing energy reserves (Bay et al., 1996; Alcoverro et al., 2001).

Irradiance is the main factor limiting seagrass vertical distribution, affecting shoot growth and productivity, and inducing changes at population level (e.g., Duarte, 1991; Olesen et al., 2002; Ralph et al., 2007). In temperate regions, light energy limitation of eelgrass growth is most pronounced for deep-adapted populations where irradiance allows seagrasses a marginally positive carbon budget on an annual basis (Dennison, 1987). At intermediate latitudes, eelgrass meadows at greater depth are generally characterized by low shoot densities, but greater shoot weights and wider leaves than shallow meadows, although peaks in shoot weight were also commonly observed at intermediate depths (i.e., Krause-Jensen et al., 2000; Olesen et al., 2017). Such an adaptive strategy allows plants to reduce self-shading and achieve higher light absorption, thus favouring a deeper colonization (Krause-Jensen et al., 2000).

Distributed in the middle of its latitudinal range (51°–55°N), *Z. marina* is the most dominant subtidal seagrass in Ireland which can colonize maximum depths of 10 m (NPWS, 2014; MERC, 2005). However, only few studies have, even peripherally, addressed Irish eelgrass population ecology (Dale et al., 2007; Jones and Unsworth, 2016; Wilkes et al., 2017). Ireland's climate is defined as a temperate oceanic climate, characterized by clearly defined climatic periods with a lack of extreme cold or warm temperatures (https://www.met.ie; Peel et al., 2007). Due to their relative inaccessibility and the generally low anthropogenic impacts in remote coastal areas in western Ireland, large undisturbed seagrass meadows may have persisted until the present day.

We hypothesize that Irish eelgrasses may show a discernible temporal pattern regarding shoot growth and population dynamics as Ireland is characterized by distinct, environmentally defined, seasons. Secondly, we propose that low-light conditions at greater depth induce changes in vegetative development. In addition, we propose that annual leaf formation rates and above-ground biomass production in Irish populations is related to local surface water temperatures and follow large-scale longitudinal trends. Therefore, the objectives of this study were to characterize the temporal changes of plant descriptors at shoot and population level in three meadows in populations from western Ireland. Adaptations to depth-related environmental conditions were assessed by comparing temporal performance of plants from different depths. Finally, we evaluated the annual leaf formation rate and above-ground biomass across their geographical distribution range (27° – 66 °N) in relation to in situ summer and annual seawater surface temperatures (SST).

2. Materials and methods

2.1. Study sites

Of the three *Z. marina* populations studied in western Ireland, two were located in Kilkieran Bay, northern Galway Bay, i.e., Lettermore (LM) (53°17′58″ N, -9°42′43″ W) and Tír an Fhia (TI) (53°15′37.5″ N, -9°38′28.8″W). The third population was situated at Finavarra (FV) (53°8′50″ N, -9°07′43″W), southern Galway Bay. These populations were chosen due to their current protected status, their remoteness and their low exposure to anthropogenic disturbances (NPWS, 2014). All the three sites are (i) characterized as Special Areas of Conservation (SAC), (ii) Natural Heritage Areas (NHAs), which are considered important for the habitats present or areas which hold species whose habitats require protection (www.npws.ie), and (iii) classified as "unpolluted" areas by the Irish Environmental Protective Area (EPA) (NPWS, 2014). In addition, the selected coastal areas are recognized with the higher environment status regarding different biological and chemical parameters, such as, phytoplankton status, dissolved oxygen concentration or nutrient concentration, demonstrating the low anthropogenic impact in these *Z. marina* meadows (www.epa.ie). Therefore, we classified the three seagrass populations studied as 'near-pristine'.

The western Irish coastline is characterised by intertidal ranges of 4–5 m; *Z. marina* extends typically to depths of 5–6 m below mean water level (http://www.sailing.ie/). Co-occurrences of *Z. marina* and maerl were previously recorded in Kilkieran Bay (NPWS, 2014). The eelgrass meadow at TI was located along a channel, and had an estimated length of 2.5 km and a maximum width of 0.43 km. The meadow at LM extended over 3.2 km x 0.8 km and was located close to the mouth of a channel, yet it was a sheltered site protected by a group of islands which reduced hydrodynamic forces such as current velocity and wave action (NPWS, 2014). The meadow at FV was located in a shallow and sheltered bay which contained several smaller, patchy meadows; the meadow chosen for this study had an estimated size of 0.5 km × 0.2 km (Fig. 1).

2.2. Sampling procedure

Two 50 m-long permanent transects (T1 and T2) were placed in each meadow. At TI and FV, transect one (T1) was placed closer to the shoreline, while transect two (T2) was located 20 m from T1. At these sites, both transects were situated at a depth of 2–2.5 m within the same meadow, representing similar environmental conditions. By contrast, at LM, T1 was placed at 2–2.5 m, while T2 was located 30 m from T1 at 4.5–5 m, thus representing the upper and lower limits of this meadow, respectively. Only studied one meadow with a deep distribution was studied due to the scarcity of deep meadows in the area, and physical and logistical difficulties associated with access. Eelgrass monitoring was carried over four seasons (spring, summer, autumn, winter: April, July and November 2015, and January 2016), either on foot during exceptional low tides, or by snorkelling or SCUBA diving during normal tides.

2.2.1. Environmental variables and sedimentological analysis

Temperature (°C) data for Kilkieran Bay (TI and LM) were provided by the Marine Institute (http://www.marine.ie/Home/). Seawater temperatures for FV were obtained by using a submersible HOBO temperature logger (U22-001, Onset) which was placed just beside the meadow at ca. 2 m depth. This logger recorded data over two seasons (spring and summer 2015). Daily light measurements were obtained using a light sensor (Li-1400, Li-Cor, USA) located on the roof of the

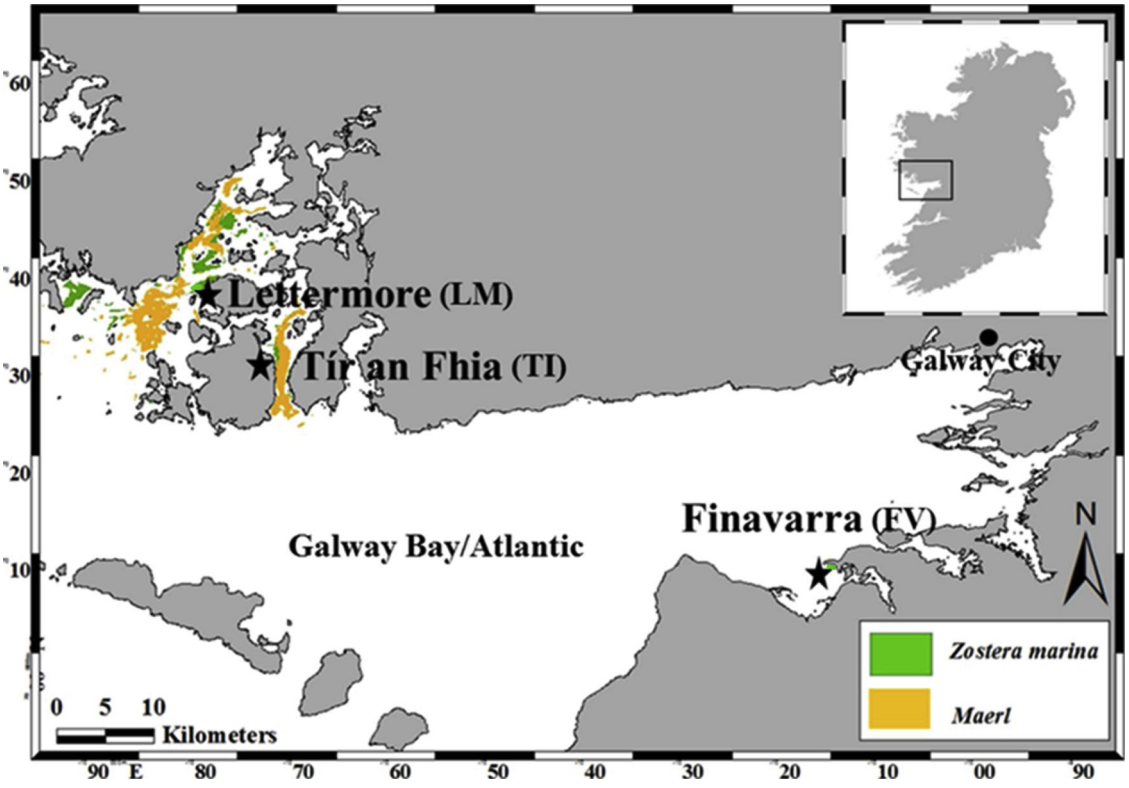

Fig. 1. Map of study area in western Ireland with locations of the three eelgrass meadows at Lettermore (LM), Tír an Fhia (TI) and Finavarra (FV), and Galway City. Eelgrass (*Zostera marina)* distribution is represented in green, and maerl presence in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Ryan Institute, NUI Galway (53°16′43″ N 9°03′40″ W, Galway City, about 25 km from FV and 40 km from LM and TI, Fig. 1). Total daily irradiance was calculated as mol photons m^{-2} d^{-1}. Additionally, at each site during sampling days, one Odyssey integrating PAR sensor (Dataflow Systems PTY Limited) was deployed in the sediment, and the irradiance sensor was oriented vertically at a 90° angle in relation to the seafloor. Loggers recorded underwater in situ instant irradiance (μmol photon m^{-2} s^{-1}) every 15 min for 1–2 hours on each sampling occasion. Sediments for grain size analysis were collected from the *Z. marina* beds in July 2015 along the two permanent transects (T1 and T2) at each location.

Grain size was determined according to the protocol described by Folk (1974); samples were carefully removed with shovel from the sediment surface to a depth of 10 cm (n = 5) and transported to the laboratory in plastic bags. The granulometry was determined following dry-sieving after repeated (n = 3) washing of samples with distilled water to remove sea salts, and subsequent oven-drying at 70 °C. Data for grain size were analyzed using GRADISTAT software (Blott and Pye, 2001; Folk and Ward, 1957).

2.2.2. Seagrass meadow characteristics: above-ground and below-ground biomass, vegetative and reproductive shoot density, and percentage cover

On each sampling occasion (April, July, November 2015 and January 2016), above-ground (AG) biomass (leaves and sheath) was determined by collecting all biomass in four random quadrats (sized 0.33 m × 0.33 m; n = 4) along the 50 m transect. Data were then normalized per m^2. Below-ground (BG) biomass (roots and rhizomes) was collected, on two occasions during the study period (July-2015 and January-2016) to minimise the disturbance of the meadows, in three random locations along the 50-m transect by collecting all the biomass contained in a quadrat (sized 0.33 m × 0.33 m; n = 3). Again, BG data were normalized per m^2. In each case, AG and BG biomass was harvested by hand using a shovel and placed into a mesh bag; once in the laboratory, remaining sediment, dead material and epiphytes were carefully removed. Plant parts were then divided into AG and BG compartments, respectively. AG material was kept for subsequent analysis. All samples were oven-dried at 60 °C for 48 h and subsequently weighed (Short, 2001).

Vegetative and reproductive shoot densities were also determined on each sampling occasion (April, July, November 2015 and January 2016). To determine vegetative and flowering shoot density, we counted all the shoots within a quadrat (sized 0.5 m × 0.5 m; n = 3) randomly placed along each 50 m transect. Density data were normalized per m^2. In parallel, flowering frequency was calculated as the number of reproductive shoots relative to total shoot density within the three quadrats along both transect within each location (Olesen et al., 2017).

Eelgrass and maerl percentage cover was assessed by taking 10–12 random underwater photographs of the 0.5 m x 0.5 m quadrat along the permanent transects (T1 and T2) at each location, using a water-proof camera SJCAM sj4000. To estimate the percentage cover of *Z. marina* and maerl, a grid of 10 × 10 (= 100) points was overlaid onto each picture, and points enclosed in the grid with the presence of macrophytes were counted visually on a computer screen (Winters et al., 2011).

2.2.3. Morphometric descriptors at shoot level

At each site, shoot characteristics were assessed using all the shoots harvested to estimate the AG biomass (n = 4) (*see above for details*). Shoots were transported to the laboratory where we measured (i) mean shoot biomass (leaf and sheath biomass) (g DW), (ii) mean shoot length (up to the tip of the longest leaf in the shoot) (cm), (iii) mean number of leaves per shoot, and (iv) mean leaf width per shoot (mm). Leaf width was determined mid-way between the base and the tip of the second youngest leaf. In addition, canopy height was assessed by using the 10 longest shoots per quadrat (n = 4) (Longstaff and Dennison, 1999).

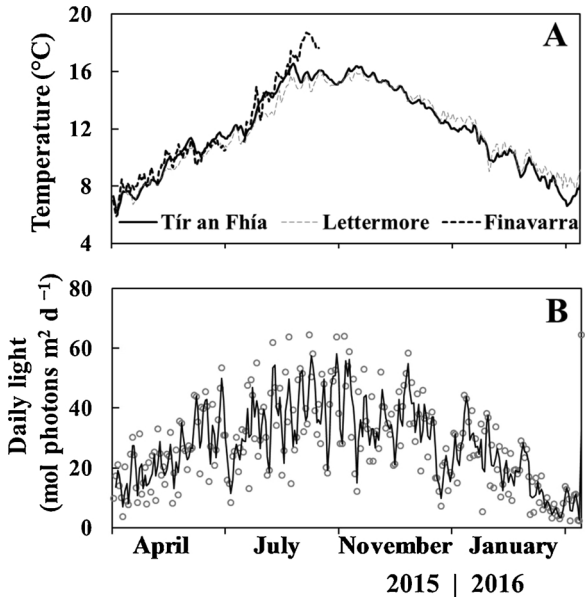

Fig. 2. Daily seawater temperature in the shallow eelgrass meadow at Lettermore (LM), Tír an Fhia (TI) and Finavarra (FV) (A). Measurements of daily light (PAR; mol photons m^{-2} d^{-1}) measured on the roof of the Martin Ryan Building (B), NUI Galway, Galway City (see Fig. 1).

From these (longest) shoots we calculated (i) shoot biomass (g DW), (ii) mean shoot length (cm) and (iii) mean leaf width per shoot (mm).

2.2.4. Annual biomass production and latitudinal comparison

The annual leaf formation rate was determined by reconstructing the seasonal growth cycle of the annual number of rhizome internodes following the methodology described by Olesen et al. (2015, 2017). To determine the annual recent past rhizome formation, in September 2015, 8–10 healthy apical shoots were collected haphazardly over a distance of 5–10 m throughout each transect to avoid potential pseudo-replication. We carefully collected the green part of the shoots and the longest and intact rhizome. Lateral shoots (rhizome branches) were removed (when present) from the apical shoot and excluded from subsequent analyses. In temperate regions, *Z. marina* develops longer and greater numbers of rhizome internodes during warmer months than during the winter period (i.e., Sand-Jensen, 1975). Thus, by measuring changes in the length of the rhizome internodes of the collected apical shoots, we calculated the number of internodes produced in the last year (from autumn 2014 to autumn 2015). Annual leaf formation rate was assumed as a 1:1 relationship between rhizome segment formation and leaf formation (Sand-Jensen, 1975; Duarte et al., 1994; Olesen et al., 2015). In addition, with the selected rhizome biomass used to assess the number of internodes produced annually (internodes $shoot^{-1}$ yr^{-1}), we measured (i) the total length of the rhizome produced annually from the apex to the oldest internode (cm $apex^{-1}$ $year^{-1}$) and (ii) the weight of the selected rhizome and roots biomass produced annually (g DW $apex^{-1}$ yr^{-1}).

BG biomass and annual leaf formation rates from the three Irish eelgrass populations were compared with data of *Z. marina* across its latitudinal distribution range, and related to site-specific summer (June to August) and annual seawater surface temperatures (SST). Results were compared with those reported by Olesen et al. (2015) and more recent publications. SST data for the latitudinal comparison were derived from the Bio-ORACLE database (http://www.bio-oracle.org) (Tyberghein et al., 2012) with a resolution of 0.5 km^2.

2.3. Statistical analysis

Firstly, we compared differences between T-1 and T-2 applying *t*-test ($p < 0.05$) in the three locations studied (LM, TI and FV). Subsequently, prior to conducting statistical analyses, homogeneity and normality of data were tested using Levene's test and the Kolmogorov–Smirnov test, respectively (Sokal and Rohlf, 1995). Data that did not pass the tests were then ln transformed. As data did still not meet the required criteria, to study temporal and location patterns and acclimations to different depth gradients at shoot and population level, the non-parametric method PERMANOVA was performed. We developed two PERMANOVA models; the first model was run to assess temporal and location effects at population and shoot level, comparing all the shallow meadows (2–2.5 m) which included: LM-T1, TI (T1 and T2) and FV (T1 and T2). We used "month" as fixed factor and "location" as random factor. The second model was performed to assess temporal and depth effects at shoot and population level, comparing shallow (LM-T1) versus deep populations (LM-T2). Here, we used both "month" and "depth" as fixed factors. *T*-test was applied to assess significant differences ($p < 0.05$) between specific months and locations. Pearson's linear regressions were applied to assess potential correlation between morphological and population descriptors. Additionally, to explore and visualize temporal differences in the morphological variability (shoot biomass, shoot length, leaf width and canopy height) between shallow and deep-adapted populations, we used (i) the coefficient of variation (CV), (ii) alongside the flexible ordination technique principal coordinate analysis (PCO) and (iii) the distance-based test for homogeneity of multivariate dispersion (PERMADISP). Both statistical techniques, PCO and PERMADISP, were based on a Euclidean similarity matrix. Before performing PCO and PERMADISP analyses, data was standardized to ensure the same contribution of each morphological variable. Significant differences between locations (LM-T1, LM-T2, TI and FV) regarding the annual rhizome production and annual leaf formation were examined using *t*-test. All statistical analyses were carried out using the statistical package IBM SPSS Inc., v.13 and PRIMER & PERMANOVA 6.

3. Results

3.1. Environmental variables and sedimentological analysis

At all three locations on the Irish west coast, maximum seawater temperature peaked in summer (July), with average values of 15.6 ± 0.4 °C; whereas, summer maxima at FV (17.6 ± 0.9 °C) were two degrees warmer than at TI and LM (Fig. 2, Table 1). For the rest of the year, temperatures at the three locations were similar. Lowest (6–7 °C) temperatures were attained in winter, and intermediate temperatures (10–12 °C) in spring and autumn. Maximum (surface) irradiance coincided with temperature peaks, reaching highest values of 40.9 ± 14.2 mol photons m^{-2} d^{-1} in summer, and minimum values of 11.1 ± 7.4 mol photons m^{-2} d^{-1} occurred in winter. Moreover, annual underwater in situ instant irradiances measured during sampling in shallow populations LM-T2 (10.3 µmol photon m^{-2} s^{-1}) was 75.5% lower than in populations at the shallowest area, LM-T1 (42.1 µmol photon m^{-2} s^{-1}) (Table 1).

The three locations were characterized by intermediate sediment grain size, ranging from 0.56 mm to 0.75 mm. Sediments of both transects of LM (LM-T1 and LM-T2) contained the highest percentage of mud, with an average value of 5.0 ± 0.3% (Table S1). Also, LM-T2, was characterized by the highest percentage of gravel (1.69 mm), which was related to the occurrence of maerl.

Table 1
Geographic coordinates of the permanent transects (T1 and T2) at each location (LM, TI and FV) (water depth of each transect relative to the mean water level). Seawater temperature measured at times when *Z. marina* biomass was collected. in situ irradiance (PAR, μmol photon m^{-2} s^{-1}) was measured at each location during sampling.

	LM-T1	LM-T2	TI-T1	TI-T2	FV-T1	FV-T2
Latitude	53.299146	53.299364	53.260786	53.260775	53.147562	53.147086
Longitude	−9.712050	−9.713681	−9.641136	−9.641533	−9.128845	−9.128813
Depth (m)	[2–2.5]	[4.5–5]	[2–2.5]	[2–2.5]	[2–2.5]	[2–2.5]
Temperature (°C)						
April	11	11	10	10	11	11
July	16	15	15	16	17	17
November	12	11	11	11	11	11
January	7	7	7	7	6	6
Irradiance (μmol photons m^{-2} s^{-1})						
April	66.8 ± 19	15 ± 0.6	93.7 ± 48.0	93.7 ± 48.0	71.7 ± 6.8	71.7 ± 6.8
July	43.5 ± 15.10	14.8 ± 4.2	60.0 ± 11.3	60.0 ± 11.3	63.0 ± 15.7	63.0 ± 15.7
November	38.8 ± 20.8	7.1 ± 2.7	35.0 ± 5.8	35.0 ± 5.8	18.4 ± 5.5	18.4 ± 5.5
January	19.3 ± 8.1	4.3 ± 0.6	37.5 ± 16.0	37.5 ± 16.0	45.3 ± 9.9	45.3 ± 9.9

3.2. Morphometric descriptors at shoot level

Overall, results showed that in the majority of cases there were no significant differences in descriptors between TI-T1 and TI-T2, nor between FV-T1 and FV-T2 over the study period (*t*-test, $p < 0.05$); hence, in these locations, data from both transect (T1 and T2) were combined (Tables 2 and 3, Fig. 3). Morphological assessment highlighted a significant temporal variability, in terms of shoot biomass, shoot length and leaf width in all populations, with higher values attained in July, followed by November and April, and lower values observed in January, at all locations (Table 2). (Fig. 3A–C) (PERMANOVA, $p < 0.001$, Table 5). In TI, FV and LM-T1, shoot biomass increased by a significant 111.8%, 81.4% and 183.3% respectively, from January to July, while shoot length increased by 76.5% in TI, 91.4% in FV and 49.1% in LM-T1 (Fig. 3A–C). Average data for leaf width from all shallow transects (TI, FV and LM-T1) indicated slight, but significant, temporal variability with generally, on average, broadest leaves were observed in July (4.8–6.5 mm), followed by November (4.6–5.5 mm) and April (4.1–5.3 mm), and finally the most narrow leaves in January (3.7–4.9 mm) (Table 2). Also, there was a significant interaction between month and location, indicating that the morphological descriptors in the populations studied were affected differently by temporal changes (PERMANOVA, $p < 0.05$, Table 5). For example, the highest annual average canopy height was observed in TI (69.8 ± 20.1 cm shoot^{-1}), followed by LM-T1 (68.6 ± 9.2 cm shoot^{-1}), and the lowest in FV (55.8 ± 11.3 cm shoot^{-1}) (Table 2).

In general, results highlighted significant morphological differences between plants living at different depths over the study period (PERMANOVA, $p < 0.05$, Table 6). Shoot length, biomass and leaf width showed significantly higher annual average values for plants at the deepest location (LM-T2) than for those from the shallowest depth (LM-T1) (Table 2, Fig. 3A–C). Largest differences in the morphological descriptors between LM-T1 and LM-T2 where usually observed in July, whereas smallest differences were reported in January (Fig. 3A–C). For instance, in July, the canopy height from LM-T2 (103.5 ± 15.1 cm shoot^{-1}) was 25.6% higher than in LM-T1 (82.4 ± 6.0 cm shoot^{-1}), while in January values were similar (Table 2). Leaves of plants receiving lower irradiances (Table 1) were 20.1% wider than those from shallower parts over the study period (Fig. 3C). PCO analysis showed that populations from deeper areas (LM-T2) displayed a higher temporal morphological variability than those from shallower parts (LM-T1) (Fig. 5). Results of shoot biomass and shoot length from LM-T2

Table 2
Temporal changes of *Zostera marina* at the three shallow (LM-T1, TI and FV (2–2.5 m)) and deep (LM-T2 (4.5–5 m)) adapted populations (see Fig. 1 for data sources) in shoot morphometric: mean shoot biomass, mean shoot length, mean leaf width and mean canopy height (10 largest shoots). Data represented as mean ± standard deviation (n = 4 or 8).

	Population	CV (%)	April	July	November	January
Shoot morphometries						
Shoot biomass	LM-T1	**23.0**	0.28 ± 0.03	0.41 ± 0.07	0.36 ± 0.5	0.22 ± 0.03
(g DW shoot^{-1})	LM-T2	**41.5**	0.43 ± 0.10	0.88 ± 0.18	0.78 ± 0.11	0.28 ± 0.03
	TI	**39.3**	0.24 ± 0.13	0.51 ± 0.16	0.41 ± 0.07	0.18 ± 0.03
	FV	**28.8**	0.24 ± 0.03	0.36 ± 0.06	0.36 ± 0.06	0.17 ± 0.04
Shoot length (cm shoot^{-1})	LM-T1	**18.5**	41.7 ± 5.6	65.3 ± 4.8	56.2 ± 8.1	43.8 ± 0.9
(cm shoot^{-1})	LM-T2	**28.4**	43.2 ± 6.7	80.9 ± 13.2	73.1 ± 8.7	43.5 ± 3.5
	TI	**28.2**	39.3 ± 6.8	71.4 ± 14.6	63.8 ± 7.8	37.3 ± 6.2
	FV	**21.8**	38.7 ± 2.8	58.6 ± 11.0	42.9 ± 2.3	33.2 ± 7.1
Leaf width	LM-T1	**10.1**	4.6 ± 0.2	5.2 ± 0.2	4.7 ± 0.1	3.9 ± 0.2
(mm shoot^{-1})	LM-T2	**10.6**	5.3 ± 0.3	6.5 ± 0.5	5.5 ± 0.2	4.9 ± 0.2
	TI	**10.0**	4.1 ± 0.1	4.8 ± 0.5	4.6 ± 0.1	3.7 ± 0.2
	FV	**16.2**	4.9 ± 0.2	6.3 ± 0.6	5.4 ± 0.7	4.0 ± 0.4
Canopy height	LM-T1	**13.4**	59.4 ± 5.1	82.4 ± 6.0	71.5 ± 4.2	61.2 ± 6.5
(cm shoot^{-1})	LM-T2	**28.7**	62.1 ± 7.2	103.5 ± 15.1	90.4 ± 14.3	48.5 ± 5.9
	TI	**28.8**	53.3 ± 4.6	96.1 ± 16.2	82.3 ± 8.5	47.5 ± 7.8
	FV	**20.2**	50.4 ± 5.1	74.4 ± 5.1	53.9 ± 3.4	44.5 ± 5.5

Bold values indicate significant differences.

Table 3
Temporal changes of *Zostera marina* at the three shallow- (LM-T1, TI and FV (2–2.5 m)) and deep- (LM-T2 (4.5–5 m)) adapted populations (see Fig. 1 for data sources) in vegetative and reproductive shoot densities (n = 3 or 6), percentage cover (n = 10 or 24), above-ground (n = 4 or 8), and below-ground biomass (n = 3 or 6), and AG/BG ratio (n = 3 or 6) at each month at the three locations. Data are presented as mean ± standard deviation.

Population descriptors	Population	CV (%)	April	July	November	January
Vegetative shoots (no. m^{-2})	LM-T1	**19.0**	165.3 ± 23.2	269.3 ± 15.4	184 ± 34.4	206.8 ± 68.2
	LM-T2	**9.3**	62 ± 24.1	69.2 ± 24	78.6 ± 20	64.1 ± 28.1
	TI	**18.5**	185.4 ± 17.6	248.2 ± 62.1	148.6 ± 23.6	188.1 ± 34.4
	FV	**9.2**	193.2 ± 29.1	236.1 ± 46.2	194.8 ± 43.3	229.9 ± 32.2
Reproductive shoots (no. m^{-2})	LM-T1	**115.1**	2.0 ± 0.4	5.2 ± 0.4	0.09 ± 0.04	0.0
	LM-T2	**144.4**	0.3 ± 0.1	2.0 ± 0.1	0.0	0.0
	TI	**146.2**	0.8 ± 0.5	5.8 ± 1.7	0.0	0.0
	FV	**80.7**	0.5 ± 0.2	0.7 ± 0.8	0.16 ± 0.06	0.0
Cover (%)	LM-T1	**17.3**	65.9 ± 20.5	97.2 ± 5.1	77.1 ± 18.6	64.1 ± 8.5
	LM-T2	**30.8**	18.4 ± 17.5	44.4 ± 23.0	35.0 ± 19.1	27.2 ± 10.5
	TI	**15.7**	77.9 ± 13.2	91.1 ± 10.2	64.4 ± 17.7	62.3 ± 19.4
	FV	**11.4**	81.6 ± 17	81.4 ± 50.9	72.9 ± 28.8	60.9 ± 15.7
Above-ground biomass (g DW m^{-2})	LM-T1	**37.3**	49.7 ± 4.7	116.8 ± 6.0	67.2 ± 5.2	53.4 ± 7.5
	LM-T2	**41.1**	33.4 ± 8.3	64.3 ± 8.7	63.5 ± 4.5	21.3 ± 5.5
	TI	**51.4**	46.7 ± 9.1	128.5 ± 6.0	61.9 ± 7.5	38.5 ± 10.2
	FV	**32.1**	48.6 ± 11.4	92.1 ± 9.2	70.8 ± 7.5	40.2 ± 3.9
Below-ground biomass (g DW m^{-2})	LM-T1	**16.8**	nd	244.1 ± 22.6	nd	202.04 ± 32.8
	LM-T2	**3.7**	nd	38.4 ± 18.8	nd	41.31 ± 9.3
	TI	**5.3**	nd	168.8 ± 41.8	nd	187.8 ± 43.6
	FV	**23.8**	nd	209.6 ± 62.6	nd	129.1 ± 42.8
A/B ratio	LM-T1	**29.7**	nd	0.48 ± 0.01	nd	0.26 ± 0.02
	LM-T2	**52.5**	nd	1.67 ± 0.8	nd	0.52 ± 0.1
	TI	**58.3**	nd	0.76 ± 0.2	nd	0.20 ± 0.01
	FV	**17.3**	nd	0.44 ± 0.3	nd	0.31 ± 0.1

Bold values indicate significant differences.

displayed a markedly higher temporal dispersion than LM-T1 (PERMADISP, $p < 0.05$, Table 7), and also showed a larger temporal coefficient of variation (CV) (Table 2).

Throughout the study period, temporal variability in shoot biomass (Fig. 4) was positively correlated with changes in shoot length and leaf width; for instance, shoot biomass was correlated with shoot length ($R^2 = 0.8$, $p < 0.001$, Fig. 4A) and leaf width ($R^2 = 0.5$, $p < 0.05$, Fig. 4B).

3.3. Seagrass meadow characteristics: above-ground biomass, vegetative and reproductive shoot density, and percentage cover

AG biomass differed temporally at all locations, with significantly higher values observed in summer, followed by intermediate values in spring and autumn, and lowest in winter (PERMANOVA, $p < 0.01$, Table 6) (Fig. 6). In LM-T2, significantly lower values of AG and BG biomass were observed than in LM-T1 (Table 3). Also, there were significantly higher AG/BG ratios in deep populations compared to shallow ones, which was particularly pronounced in summer (LM-T1 = 0.48 ± 0.01; LM-T2 = 1.67 ± 0.8) (Table 3). Shoot density significantly varied among months, with a slightly higher density determined in July (Fig. 5). Similarly, the number of shoots was significantly affected by depth (PERMANOVA, $p < 0.001$, Table 6), with *Z. marina* plants at the deepest site (LM-T2) characterized by lower annual average densities of 68.5 ± 6.4 shoots m^{-2} than plants at LM-T1 (206.4 ± 39.2 shoots m^{-2}) (Fig. 6A). Eelgrass percentage cover was influenced by temporal changes (PERMANOVA, $p < 0.05$, Table 6), with maximum average (LM-T1, TI and FV) values of 87.8 ± 6.6% attained in summer, and a minimum of 60.6 ± 4.7% observed in winter (Fig. 6C). Also, seagrass cover changed significantly with depth (PERMANOVA, $p < 0.01$, Table 6), with LM-T1 showing annual average values of 76.1 ± 6.5%, compared to 34 ± 4.5% in LM-T2. Furthermore, the presence of maerl was only observed at greater depth (LM-T2) with coverage of around 67.1 ± 15.3% of the seafloor, which became more widespread at greater depths (*pers. obs.*) (Figs. 6 and S3).

In shallow populations, temporal changes in AG biomass were positively correlated with changes in shoot abundance ($R^2 = 0.4$, $p < 0.05$) and also with percentage cover ($R^2 = 0.4$, $p < 0.05$). In addition, temporal changes in AG biomass was positively correlated with shoot biomass ($R^2 = 0.7$, $p < 0.001$) and shoot length ($R^2 = 0.8$, $p < 0.001$), and percentage cover was positively correlated with shoot biomass ($R^2 = 0.4$, $p < 0.05$) shoot length ($R^2 = 0.4$, $p < 0.05$).

The presence of reproductive shoots significantly changed temporally, with higher densities observed in July (14–17 °C) (PERMANOVA, $p < 0.05$, Table 6). At this time, the highest density of reproductive shoots was documented, with plants developing both mature male and female flowers, and seeds. Only sporadic reproductive shoots were observed in autumn, and no reproductive plants were found in winter. Also, the density of reproductive shoots varied significantly (PERMANOVA, $p < 0.001$) between locations, with the larger meadows, LM-T1 (5.2 ± 0.8 shoot m^{-2}), TI (5.8 ± 1.7 shoot m^{-2}) producing 4 - 6-times more than smaller beds at FV (0.7 ± 0.3 shoot m^{-2}) (Fig. 5). In July, deep-adapted populations (LM-T2) had a density of flowering shoots of 2.0 ± 1.1 m^{-2}, representing 2.9% of the total number plants collected, compared 0.3–2.3 % of plants from shallow populations.

3.4. Annual rhizome production

Marked differences (*t*-test, $p < 0.05$) in rhizome production among sites were observed, with higher number of internodes produced per year in FV meadows (29.2 ± 1.5 internodes $shoot^{-1}$ yr^{-1}), followed by LM-T1 (23.3 ± 1.8 internodes $shoot^{-1}$ yr^{-1}) and TI (20.0 ± 1.5 internodes $shoot^{-1}$ yr^{-1}), and lowest values observed in the deepest population (LM-T2, 15.1 ± 1.3 internodes $shoot^{-1}$ yr^{-1}). Highest annual rhizome biomass production was observed in FV (1.7 ± 0.45 g DW $shoot^{-1}$ yr^{-1}) (*t*-test, $p < 0.05$), followed by LM-T1 (0.97 ± 2.5 g DW $shoot^{-1}$ yr^{-1}) and lowest values in plants from the deepest area (LM-T2, 0.60 ± 0.13 g DW $shoot^{-1}$ yr^{-1}) (Table 4). The highest annual elongation rate of the rhizome occurred in TI (16.79 ± 4.46 cm $apex^{-1}$ $year^{-1}$) whereas lowest values were observed in plants from LM-T2

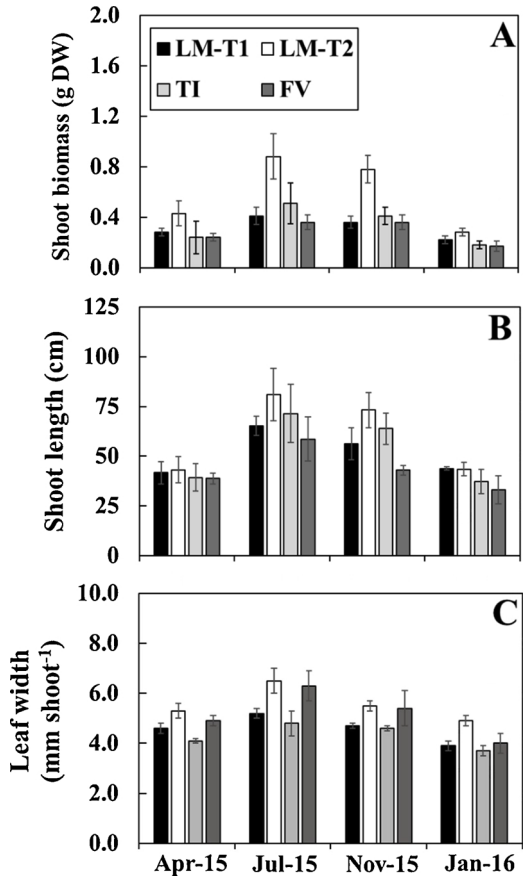

Fig. 3. Temporal changes in *Zostera marina* shoot morphometric parameters at the three locations (LM, TI, FV): mean shoot biomass (A) mean shoot length (B) and mean leaf width (C) (n = 8). At LM, samples were collected at different depths (LM-T1 (2–2.5 m) and LM-T2 (4.5–5 m)) (n = 4). Data represent mean ± standard deviation.

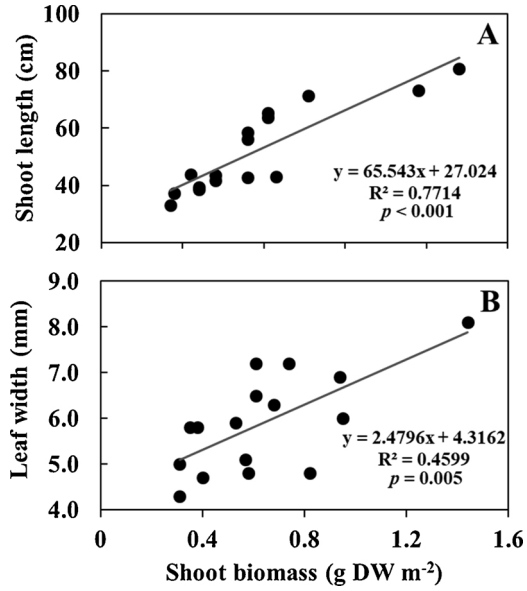

Fig. 4. Mean shoot length (Y-axe) versus mean shoot biomass (X-axe) (Panel A) in the three locations in western Ireland, LM-T1, LM-T2, TI and FV; mean shoot length (Y-axe) versus mean leaf width (X-axe) (Panel B). Black lines represent the linear regression line (n = 16).

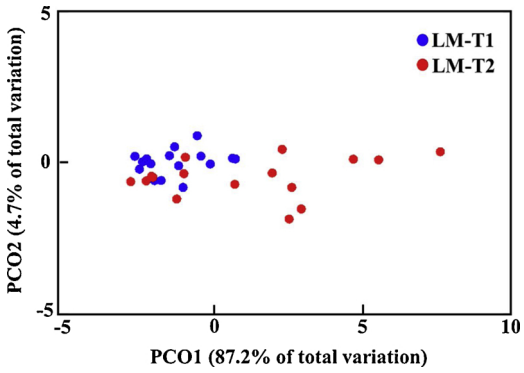

Fig. 5. Results of PCO contrasting the dispersion of the morphological characteristics including mean shoot biomass, mean shoot length, mean leaf width and canopy height (data in Table 2) from shallow-adapted populations LM-T1 (2–2.5 m) versus deep adapted-population LM-T2 (4.5–5 m).

(13.19 ± 1.44 cm apex^{-1} year^{-1}) (*t*-test, $p < 0.05$) (Table 4).

4. Discussion

This study represents the first assessment of temporal, morphological and population characteristics of *Z. marina* populations in Ireland. We report significant temporal, site and depth-associated differences in individual shoot attributes and population descriptors; all of which represent baseline data for future monitoring efforts to measure impacts of local stressors or even global climate change effects.

4.1. Temporal changes of Irish eelgrass meadows

Results revealed a discernible temporal pattern of shoot growth and population dynamics (i.e., Baden and Pihl, 1984; Olesen and Sand-Jensen, 1993). Values for shoot length, shoot biomass, density, and percentage cover were higher during warmer and brighter months (July), mid-range in November and April, and lowest in January. For instance, shoot biomass and length were generally 2- to 3-fold greater in July than in January. Similar vegetative growth patterns were commonly observed for other cold-adapted *Z. marina* meadows in the Atlantic region (i.e., Harrison and Mann, 1975; Jacobs, 1979; Baden and Pihl, 1984; Olesen and Sand-Jensen, 1993; Beal et al., 2004). Temporal changes in shoot biomass were most likely related to ambient changes in light and temperature conditions, suggesting a direct response of *Z. marina* by adjusting leaf structures (e.g., development of larger and wider leaves) during conditions more suitable for photosynthetic activity. By contrast, smaller and thinner leaves were produced during less favourable climatic conditions as a result of low energetic input and possibly, as a mechanism to conserve metabolic cost by decreasing respiration rates (Bay et al., 1996; Alcoverro et al., 2001). In all three Irish *Z. marina* populations, higher average shoot lengths were observed in November compared to April, while shoot density remained similar in both months. This can be explained by occurrence of seed germination (Olesen and Sand-Jensen, 1994a) and lateral shoot formation during spring (i.e., Tomlison, 1974; Jacobs, 1979) with subsequent leaf growth through November. In spite of the relatively small spatial scale of this study (< 100 km), the three populations displayed marked differences in shoot and population characteristics, which can be attributed to specific local environmental conditions such as hydrodynamic conditions or nutrient concentration in the water column, which were not specifically tested in this study.

Measurements for shoot abundance (50 to 800 shoots per m^2) were relatively low in comparison with other eelgrass beds (> 3000 shoots

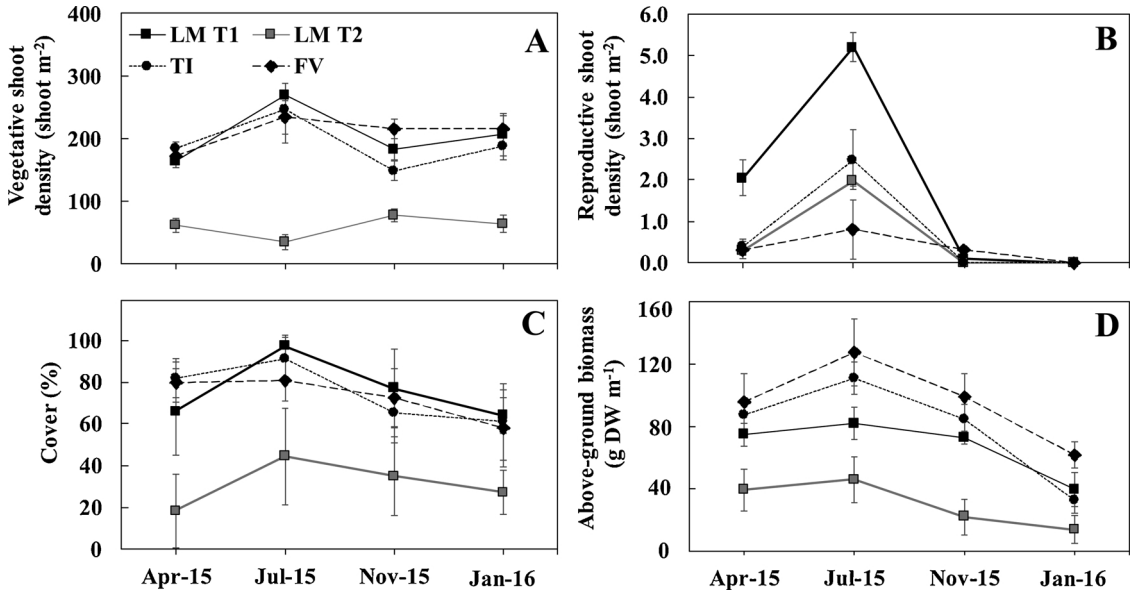

Fig. 6. Temporal changes at the three locations (LM, TI, FV) in vegetative (A) and reproductive (B) eelgrass shoots density (n = 3 or 6), eelgrass percentage cover (n = 10 or 24) (C) and above-ground biomass (n = 4 or 8) (D). At LM, samples were collected at different depths (LM-T1 (2–2.5 m) and LM-T2 (4.5–5 m)). Data represent mean ± standard deviation.

per m^2) from similar latitudes (e.g., Wium-Andersen and Borum, 1984; Krause-Jensen et al., 2000; Boström et al., 2004). Average vegetative shoot densities comparable to Irish meadows were previously observed in some cold-temperate populations which displayed larger values in warmer periods (e.g., Aioi, 1980; Olesen and Sand-Jensen, 1994b; Watanabe et al., 2005; Pihl et al., 2006), and in Mediterranean eelgrass beds (Laugier et al., 1999; Guidetti, 2000). Interestingly, the density of intertidal Irish eelgrass meadows in Kilkieran Bay (less than 5 km from LM and TI) ranged from 800 to 1300 shoots per m^2 (*pers. observation*). In addition, the reported slight temporal changes in shoot abundance in Irish meadows are in accordance with seasonal variations in shoot density for eelgrass meadows inhabiting similar climate regimes (Jacobs, 1979; Kaldy and Lee, 2007), but also with those from populations living in warmer habitats (Laugier et al., 1999). Temporal changes in percentage cover and AG biomass were positively correlated with changes in shoot morphometry (e.g. shoot biomass, shoot length) as was reported from other cold temperate *Z. marina* populations (Olesen and Sand-Jensen, 1994a). This suggests rapid production of leaf structures leading to high leaf turnover rates and a significant export of organic matter to other systems (Mateo et al., 2006; Boudouresque et al., 2000). Our data therefore indicate that individual and population descriptors in Irish eelgrass meadows correspond well to the vegetative development and growth dynamics of other perennial life-cycle temperate *Z. marina* populations inhabiting similar stable environments and characterized by dense stands of large individuals (Olesen and Sand-Jensen, 1994a; Kaldy and Lee, 2007). The influence of local environmental fluctuations, such as temperature and irradiance on the reproductive effort and flowering of *Z. marina* has been extensively documented, revealing high variability along its latitudinal distribution range (e.g., Meling-lópez and Ibarra-Obando, 1999; Harwell and Orth, 2002; Lee et al., 2006; Rollon et al., 2003). In our Irish meadows, the presence of flowering plants was observed from March-April (SST of ~10 °C) until the end of November (SST of ~10 °C) (*pers. obs.*), suggesting that the reproductive period covered nine months. By contrast, in warmer adapted populations in the Mediterranean Sea the presence of flowering shoots only lasted 4–5 months (Laugier et al., 1999). In contrast to other eelgrass populations, or indeed other seagrass species (Olesen et al., 2015; Stubler et al., 2017), we observed a higher reproductive effort in plants living at the deepest edge of the meadow. Previous studies suggested that more stressed or disturbed environments favour reproductive allocation in seagrasses (Van Lent and Verschuure, 1994; Cabaco and Santos, 2012).

4.2. Depth-related responses at shoot and population level

Our second assumption stated that the vegetative development of deep-adapted populations may differ from that of shallow populations. In this study, the parameters, such as shoot biomass and length, density, cover and AG and BG biomass, varied significantly with depth and were most likely linked to changes in irradiance profiles. Plants in the deeper transect (LM-T2) were characterized by the presence of relatively larger shoots with higher biomass compared to plants from shallower locations (LM-T1). These morphological characteristics, along with the 2- to 3-fold decreases in AG biomass, eelgrass cover and density with increasing depth, represent a widely observed trend for deep cold-temperate *Z. marina* populations at similar latitudes, as well as for other seagrass species (e.g., Lalumière et al., 1994; Olesen et al., 2002; Nielsen et al., 2002; Beca-Carretero et al., 2018a). Also, temperate *Z. marina* populations may exhibit larger shoots at intermediate depths and smaller shoots at the deepest edge of the meadow (Krause-Jensen

Table 4
Zostera marina production of annual number of rhizome internodes per shoot, annual rhizome biomass and annual rhizome elongation at the three locations collected in September 2015 (n = 8–10).

Annual production	LM-T1	LM-T2	TI-T1	TI-T2	FV-T1	FV-T2
Rhizome internodes (internodes $shoot^{-1}$ yr^{-1})	23.3 ± 1.8	15.1 ± 1.3	20.4 ± 1.5	19.0 ± 0.8	28.9 ± 1.4	29.4 ± 1.8
Rhizome biomass (g DW $apex^{-1}$ yr^{-1})	0.97 ± 0.2	0.6 ± 0.2	0.6 ± 0.1	0.6 ± 0.1	1.9 ± 0.4	1.5 ± 0.9
Rhizome elongation (cm $apex^{-1}$ yr^{-1})	15.6 ± 1.3	13.2 ± 1.4	17.1 ± 4,4	16.5 ± 1.1	15.9 ± 3.4	15.4 ± 3.5

Table 5
Results of the PERMANOVA analysis of morphological descriptors at shoot level including mean shoot biomass, mean shoot length, mean leaf width and canopy height (10 largest shoots) in response to temporal, location and depth variabilities. Pseudo F-values are shown along with significance levels (*$p < 0.05$; **$p < 0.01$, ***$p < 0.001$), and degree of freedom (df).

Shoot morphometrics			Shoot biomass (g DW shoot^{-1})		Shoot length (cm shoot^{-1})		Leaf width (mm shoot^{-1})		*Canopy height* (cm shoot^{-1})
Treatment	*df*	*MS*	*Pseudo-F*	*MS*	*Pseudo-F*	*MS*	*Pseudo-F*	*MS*	*Pseudo-F*
Month (M)	3	0.21	**29.2*****	14.4	**43.5*****	0.04	**50.9*****	0.31	**59.1*****
Location (L)	2	0.02	**3.2***	3.9	**11.7****	0.03	**35.2*****	0.08	**14.8*****
MxL	6	0.01	**1.9***	0.9	**2.6***	0.00	**3.1***	0.02	**3.8***
Residual	68	0.01		0.3		0.00		0.01	
Total	79								
Month (M)	3	1.21	**35.4****	0.63	**38.0***	0.10	**22.2****	1.32	**21.9****
Depth (D)	1	2.31	**67.6****	0.10	**6.1***	0.32	**69.8*****	0.81	**13.5****
MxD	3	0.11	**3.3***	0.04	2.1	0.002	0.4	0.34	**5.6***
Residual	24	0.03		0.02		0.005		0.06	
Total	31								

Bold values indicate significant differences.

et al., 2000). The reduction in shoot density and increase in shoot biomass with increasing depths favours vertical propagation rather that horizontal growth, a well-known photo-adaptive response to improve light absorption and reduce self-shading (i.e., Dennison and Albert, 1986; Krause-Jensen et al., 2000; Ralph et al., 2007). Low annual leaf production in deep-adapted populations can lead to lower leaf turnover rates in comparison to shallower plants, as described for *Cymodocea nodosa* populations from the Mediterranean Sea (Terrados et al., 2006). Such results could be expected as light is considered the most important controlling factor of eelgrass production and shoot morphology, abundance and population architecture, especially towards the lower depth limit of a meadow (Duarte, 1991; Olesen et al., 2002; Ralph et al., 2007). In July, deep-adapted populations (LM-T2) developed shoots with significantly greater weight and length than shallow plants (LM-T1), whereas there were no significant differences in winter. On this basis, PCO and PERMADISP analysis may suggest that light limitation induces a higher temporal morphological variability in deep populations in comparison with shallower plants (Touchette and Burkholder, 2000). Both shallow and deep Irish plants maintained leaves in winter, suggesting that some photosynthetic activity took place at this time (Evans et al., 1986; Olesen and Sand-Jensen, 1993).

The present study represents the first data on *Z. marina* AB and BG biomass for Ireland. The observed marked decreases in AG/BG ratio with increasing depth concur with previous studies on temperate *Z. marina* populations (Olesen and Sand-Jensen, 1993; Krause-Jensen et al., 2000) and other seagrass species such as *Thalassia testudinum* (et al., 2000) along a depth gradient. Differential biomass allocation between deep- and shallow-adapted *Z. marina* populations has been suggested as an adaptive mechanism to keep metabolic costs low and favour leaf production (Olesen and Sand-Jensen, 1993; Krause-Jensen et al., 2000; Nielsen et al., 2002). On the other hand, studies on *Posidonia oceanica* and *Cymodocea nodosa* demonstrated that reductions in light do not necessarily induce allocation of biomass to AG structures, therefore suggesting that this is not a common pattern across all seagrass species (Romero et al., 1998; Olesen et al., 2002; Terrados et al., 2006). The observed reductions in BG biomass, annual number of rhizome internodes and rhizome elongation can be explained by low irradiances limiting primary production and carbon balance, and thus reducing the capacity to produce and store carbon in the rhizomes (Alcoverro et al., 1995; Serrano et al., 2014).

4.3. Irish eelgrass leaf production and above-ground biomass in comparison to populations from other latitudes

Results from a detailed latitudinal comparison revealed a strong trend for annual leaves formation in *Z. marina* populations to be controlled by large-scale factors such as SST. A similar trend was observed by Olesen et al. (2014), however, in their study, annual leaf formation was only correlated with air temperature, rather than SST. Our correlations indicate a leaf formation rate of 1.0 to 1.4 leaves per increase of 1 °C in SST and 0.56 leaves per degree latitude southward (Fig. 7). Leaf production in our Atlantic Irish eelgrass populations ranged from 29.4

Table 6
Results of the PERMANOVA analysis between descriptors at population level including vegetative and reproductive shoot density, seagrass cover, above-ground (AG), below-ground (BG) biomass and AG/BG ratio in response to temporal, location and depth variation. Pseudo F-values are shown along with significance levels (*$p < 0.05$; **$p < 0.01$, ***$p < 0.001$), and degree of freedom (df).

Population descriptors			Density Vegetative S. (no. m^{-2})			Reproductive S. (no. m^{-2})			Cover (%)			AG (g DW m^{-2})			Biomass BG (g DW m^{-2})			AG/BG
Treatment	*df*	*MS*	*Pseudo-F*	*df*	*MS*	*Pseudo-F*	*df*	*MS*	*Pseudo-F*	*df*	*MS*	*Pseudo-F*	*df*	*MS*	*Pseudo-F*	*df*	*MS*	*Pseudo-F*
Month (M)	3	0.4	**7.3***	3	59.8	**4.3***	3	1.7	**9.9****	3	3.2	**28.9*****	1	0.2	**14.8****	1	0.5	4.7
Location (L)	2	0.1	1.5	2	20.4	**74.4*****	4	0.2	1.0	2	0.1	2.8	2	0.7	**11.6****	2	0.0	1.3
MxL	6	0.1	1.4	6	14.6	**53.1*****	11	0.2	1.2	6	0.1	**3.6***	2	0.0	0.2	2	0.1	3.1
Residual	68	0.04		68	0.3		201	0.3		68	0.03		24	0.1		24	0.0	
Total	79			79			219			79			29			29		
Month (M)	3	0.2	**3.9***	3	22.6	**312.3*****	3	1.2	**9.7*****	3	1.5	**46.8*****	1	0.0	0.1	1	1.4	**5.2***
Depth (D)	1	11.1	**270.9*****	1	11.9	**164.9*****	1	2.3	**79.9*****	1	1.9	**61.5*****	1	6.7	**55.1*****	1	1.6	**5.8***
MxD	3	0.7	**17.5****	3	4.4	**60.8*****	3	0.9	**4.0*****	3	0.3	**8.1****	1	0.2	1.3	1	0.7	2.5
Residual	24	0.0		24	0.1		90	0.3		24	0.03		8	0.1		8	0.3	
Total	31			31			97			31			12			12		

Bold values indicate significant differences.

Table 7
Result of PERMADISP comparing morphological responses of shallow (LM-T1) and deep adapted (LM-T2) *Zostera marina* populations including mean shoot biomass, mean shoot length, mean leaf width and canopy height (10 largest shoots). F-values are shown along with significance levels (*$p < 0.05$) and marginal significant level (°$p < 0.1 > 0.05$).

Shoot morphometrics	Shoot biomass (g DW shoot^{-1})	Shoot length (cm shoot^{-1})	Leaf width (mm shoot^{-1})	Canopy height (shoot^{-1} cm)
F	9.804	9.254	0.152	5.019
P (perm)	**0.025***	**0.049***	0.808	0.057°

Bold values indicate significant differences.

to 19.6 leaves per year, which was similar to values from other cold-adapted seagrasses as well as other populations inhabiting similar latitudinal ranges from the North Sea (i.e., 26.1 leaves shoot^{-1} yr^{-1}, Netherlands; Nienhuis and De Bree, 1980). Higher leaf formation rates were observed at the southern limits of eelgrass distribution in Mexico (22.4 °C) and in Mediterranean regions of Spain (23.2 °C) with 44.5 and 43.8 leaves shoot^{-1} yr^{-1}, respectively (Ibarra-Obando et al., 1997; Marbà et al., 1996). Yet, diebacks observed at these southern latitudes after periods of anomalously high summer temperatures indicate that their optimal physiological temperature may have been exceeded (Durako and Moffler, 1987; Reusch et al., 2005). On the other hand, the lowest leaf production rates were observed in Greenland meadows which inhabit the coldest regions, suggesting that such low temperatures limit production rates (6.9–13.1 leaves shoot^{-1} yr^{-1}, Olesen et al., 2015). Recent investigations reported that rises in SST, and reductions in the seasonal sea ice, may improve environmental conditions in favour of seagrass growth and production performance and potential dispersion (Krause-Jensen et al., 2011; Marbà et al., 2018).

Above-ground biomass was neither correlated with in situ summer nor with SST, which is in line with previous findings (Clausen et al., 2014; Olesen et al., 2015). For shallow Irish populations, AG biomass (112.5 + 15.2 g DW m^{-2}) was markedly low in comparison with published values, as Irish data did not exceed the global average values of 267.3 g m^{-2} (Fig. 7). For instance, larger AG deposits at similar latitudes were observed with values ranging from 404 to 1060 g m^{-1}

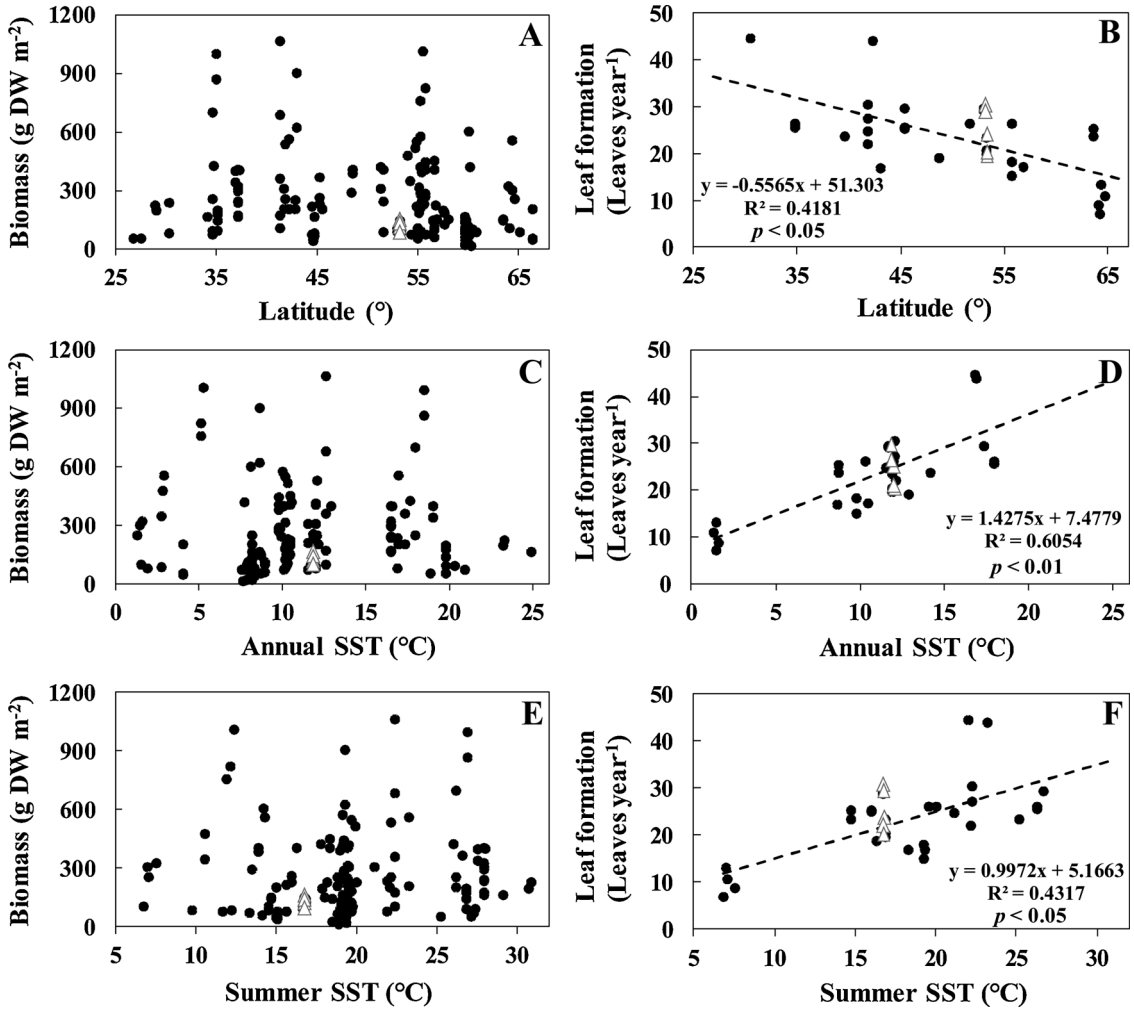

Fig. 7. Above-ground biomass and annual leaf formation rate and corresponding geographical latitudinal distribution range (Panel A and B), mean annual SST (Panel C and D) and mean summer SST (Panel E and F) from the literature (Tables S4 and S5) (circle symbols), and with results from the present study (triangle symbols). Dotted lines represent the linear regression line.

(e.g., Thorne-Miller et al., 1983; van Lent and Verschuure, 1994; Watanabe et al., 2005).

4.4. Implications for management: from local to global scale

As this is, to our knowledge, the first assessment of seagrass meadows in western Ireland, this study represents an essential baseline to (i) include biological data of near-pristine but understudied east-Atlantic populations into global assessments of *Z. marina* ecology, (ii) develop long-term monitoring programs to assess potential ecosystem degradation, and finally, (iii) monitor potential effects of climate change or depletions in water quality in the west coast of Ireland. Urban wastewater and agricultural activities have driven *Zostera* spp. loss where 29–49 % of cover disappeared over the last 25 years (e.g., Short and Wyllie-Echeverria, 1996; Baden et al., 2003). High occurrences of filamentous algae in seagrass leaves have been identified as a direct effect of water eutrophication, representing one of the major threats for seagrass survival (i.e., Baden et al., 2003). In our study we only observed testimonial filamentous algae on seagrass leaves in April, suggesting a low anthropogenic disturbance of these meadows. In the 1930's when the phenomenon "wasting disease" devastated extensive seagrass meadows in the north Atlantic on both the American and European coast, only few cases were reported in Ireland such as Lough Hyne (Co. Cork) or Blacksod Bay, Achill Island and Clew Bay (Co. Mayo), and these populations recovered rapidly and vigorously after this event (Whelan and Cullinane, 1987). It is noteworthy that in the 1990's an investigation in eastern Ireland reported critical losses of *Zostera* meadows distribution, particularly intertidal *Z. marina meadows,* due to eutrophication impacts (Madden et al., 1993). Nowadays, other Irish seagrass meadows may be also experiencing some anthropogenic pressures, such as aquaculture, nutrient inputs or physical disturbances (Jones and Unsworth, 2016; Walls et al., 2017; Wilkes et al., 2017). To date, no significant seagrass loss has been reported for Ireland, although recent research and monitoring programs may not have been robust enough to demonstrate a potential reduction in their health status and/or cover.

Deep populations of *Zostera* habitats are considered to represent key environmental indicators to assess the ecological status of transitional marine habitats (Dennison et al., 1997; Krause-Jensen et al., 2005). In Kilkieran Bay, vast extensions of co-occurrences of seagrass and maerl are commonly observed at the deepest edge of the eelgrass meadows, with banks of maerl becoming more abundant with depth (*pers. obs.*) (Fig. S3). This co-occurrence has so far only been documented from western Ireland (De Grave, 1999; NPWS, 2014) and France (Martin and Chauvaud, 2005), and is still largely uncharacterised. Maerl beds form a three-dimensional structure of nodular coralline algae which support a high biodiversity and production (Foster, 2001; Wilson et al., 2004). Also, both entities are part of the five Annex I habitats in the EU Habitats Directive (92/43/EEC) and both belong to the habitats on the Initial List of OSPAR Threatened and/or Declining Species and Habitats considered to be causes for concern (OSPAR Commission 2005). Further investigations are necessary to assess their interaction.

Finally, in the context of climate change, with southern populations experiencing population regressions due to anomalously high temperatures and Arctic populations experiencing more favourable environmental conditions (Krause-Jensen et al., 2015), the anticipated response of centrally distributed populations remains unclear (Beca-Carretero et al., 2018b). For Irish seagrass populations living at current maximum summer seawater temperatures ranging from 15 to 17 °C, projected increases of 2–3 °C by the end of this century (IPCC, 2014) may favour seagrass growth and production.

5. Conclusions

This study provides first data of vegetative development of Irish *Z. marina* populations and highlights a high morphological plasticity at both shoot and population level in response to temporal environmental variation and depth. Our results demonstrate that Irish eelgrass populations display patterns similar to those of other perennial *Z. marina* populations growing in stable environments, characterized by stable shoot densities but marked morphological variations in responses to environmental parameters. This study comprises the most detailed assessment of eelgrass populations in western Ireland to date, thus representing a vital contribution to current efforts in seagrass monitoring and management worldwide. We suggest that the meadows studied here should be considered as baseline sites for long-term monitoring efforts to assess any potential effects of environmental changes.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.aquabot.2019.02.003.

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